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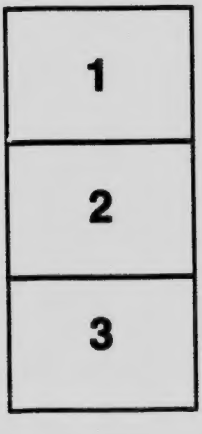

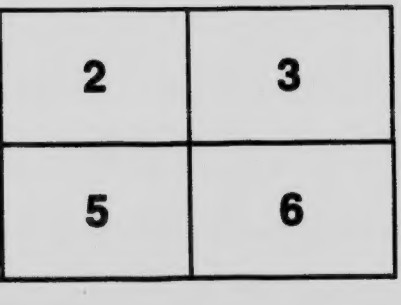

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THE EGG-LAYING HABITS OF *PLETHODON CINEREUS*

BY W H. PIERSOL, B.A., M.B.

(*Read 15th November, 1913.*)

Two accounts of the natural history of this, our commonest salamander, have appeared, one by Miss M. E. Cochran (1911) and one by the writer (1909). Both agree in their descriptions of the eggs, but neither gives any information as to the mode of deposition. The writer has sought to determine this by observations made on *Plethodon* both in its natural habitat and in a terrarium. The following is an account of the more important observations together with comment and inference. Fertilization is internal; this had been predicted in the earlier paper (1909) and has since been confirmed by the fact that a female isolated in a terrarium for four days laid eggs that developed naturally.

Case I. On one occasion the actual extrusion of the eggs was observed. The female had been placed when captured in a small glass jar along with fragments of the log in which she was found; and the jar with others containing eggs was carried back to the laboratory in a small bag. Chiefly for the sake of the eggs which are very delicate the bag was guarded from shocks as far as possible, then for another hour it stood unopened. On removing the jar from the bag it was seen that the egg laying had just begun, fortunately in such a position that all its details could be observed. The lips of the cloaca are pressed against the surface from which the eggs will eventually hang and a small quantity of mucus is extruded and adheres firmly to it. This much had been completed before observation began so nothing can be said as to the interval that then elapses before the first egg is laid. The extrusion of each egg occupies about twenty seconds and an interval of five to ten minutes occurs before the next appears. The first three eggs were laid in contact with the mucus above mentioned; the fourth, and last, adhered to them in turn through the stickiness of the egg-envelopes. As the female did not move during the entire process, all the eggs were laid at the same point, each egg as it came, crowding the preceding ones aside, thus making sure of being in contact with them. For over an hour after the last egg was laid the female did not change her position; during the next hour she left the eggs a few minutes, then returned and coiled herself about them.

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The extrusion of the egg causes it to become elongated; the greater axis may be almost twice the less. In the case above noted the spherical form was assumed within a few minutes; in other cases the elongation has taken more than an hour to disappear. Exceptionally the elongated form may be retained for a considerable time. The most extreme case met with was an egg found among natural surroundings with the longest axis 5.25 m.m. and the shortest 2.75 m.m. In the same cluster was another elongated egg, its axes being 4.0 m.m. and 3.0 m.m. The three remaining eggs were spherical; all five were in the process of gastrulation. Another egg, quite similar to the one first mentioned was laid by a female in a terrarium; it kept pace in development with the remaining eggs of its cluster up to the 50-60 cell stage. In the first two cases the segmentation cavity had formed near one end of the long axis, in the third case near one end of a short axis. As the eggs were fixed at the stages mentioned it is impossible to say how the further development would have been affected.

This mode of egg-laying places *Plethodon* at the end of a progressive series, the most primitive member being Cryptobranchus, with eggs laid in a uniform rosary-like string as described by Reese (1904) and Smith (1906). Next, as suggested by Wilder (1913), would stand *Desmognathus;* in this genus most of the eggs have left the main string of the rosary and lie at the sides of it, each retaining connection with it, however, by a short stalk. The next step is represented by such a case as *Spelerpes* (Wilder, 1899) or *Antodax* (Ritter and Miller, 1899); here the disappearance of the main string leaves each egg to be attached separately to its support—usually a stone—by a short stalk. The disappearance of this stalk for each egg, except the first, produces the separate eggs of *Plethodon*. This economy of material is highly desirable in so small an animal. The position of *Antodax* in the series given above is not that usually occupied by the genus in a series that shows progressive modification of some primitive habit; in most respects *Antodax* has departed furthest from the primitive amphibian mode of life, and *Plethodon* can only offer suggestions as to the path along which *Antodax* has travelled to its present condition. In habits, however, as in morphology, it does not follow that the higher member of a series must in every point have progressed beyond the lower.

Other observations differing from the foregoing are as follows:

Case II. In examining a terrarium on one occasion there was uncovered a female that had evidently just completed the extrusion of the eggs. Two eggs, approximately spherical, were in contact and cohering slightly; four other eggs, each more or less elongated, were lying separated from each other by intervals of about one-quarter of an inch; none

of them were suspended. Evidently under the somewhat unnatural conditions the female had moved after the extrusion of each of the last five eggs. *Case III.* In picking apart the laying log there were exposed on one occasion a female and four eggs. One of these lay by itself, markedly elongated; the other three were in contact, two of them somewhat elongated, the third apparently spherical. All four were lying on the floor of the cavity, which fortunately had been opened from the side. Examination of the female revealed the existence of four eggs in the posterior parts of the oviducts. Evidently the egg-laying process had been interrupted by the opening up of the nesting-chamber.

These last two cases have been selected from among a few of the same general character because they differ from the rest in that the eggs were not suspended. In opening up logs a few clusters have been found unattached. At first, in such cases, it was taken for granted that the opening up of the nesting-chamber had involved the loosening of the eggs. Since attention has been directed to the possibility of a cluster not having been attached, two such have been found under circumstances that would seem to preclude the idea of their having been torn from their attachment. In neither of these two cases could a stalk attached to the cluster be found. It would seem that occasionally the tendency to reduce the amount of material devoted to forming stalks for the eggs goes so far as to eliminate even the stalk of the first egg. No exact count has been kept of the number of such cases as compared with the normal, attached ones, but the impression left is that it is very small.

As might be concluded from *Case I*, an examination of the relation of the stalk to the eggs shows that it does not come from any one particular egg, but from a quantity of mucus that adheres to the outer envelope of certain of them; the impression given is that of a material poured onto the bunch, part of it being drawn out to form the stalk. As is the usual case among Urodeles the outer envelope of each egg is of a much more sticky mucus than the inner ones. Plethodon is peculiar in having this outer layer unusually thin, and in depositing a still more sticky mass of mucus before the egg-laying proper begins.

In most amphibia the impulse toward the deposition of the eggs, once these are ready for the act, is an imperative one. In some cases (*e.g.*, many frogs) the assistance of the male is needed, but generally speaking, when the proper time comes the spawn will be deposited even with conditions and surroundings that are far from natural. Both *Rana pipiens* and *Rana catesbiana* that have been kept over winter, without feeding, in a tank in the basement of the Biological Building of the University, have been known to spawn in spring and early summer respectively. (Such spawn has never developed, evidently has never

been fertilized.) In *Plethodon* the instinct is more delicately adjusted. This is shown in the marked preference for some particular log as a site for egg-laying. For instance, one small plot of woodland was found to contain *Plethodon* in abundance during the spring of 1913 and was visited on June 21st in the search for eggs. A dozen or more rotting logs yielded only males or sexually immature specimens; at last one log was found which, though apparently not differing from the others, yielded eleven females with eggs. A number of similar cases have been met with. The logs so greatly preferred are invariably conifers, but other factors must enter into the quest on for another coniferous log that seems quite similar may be close at hand yet be entirely destitute. Equally striking is the difficulty that has been experienced in getting females to lay eggs in a terrarium. The thin, almost translucent ventral wall of the abdomen allows the easy recognition of females containing eggs almost ready for deposition. If pieces of the logs in which the animals have been found are brought from the field and the pieces piled together in a terrarium so as to reconstruct roughly the log, there is no difficulty in keeping the animals alive and in good condition for long periods. They will feed readily on small insects, *e.g.*, aphids; but, like most amphibia, seem to suffer little from long deprivation. Three specimens overlooked in a small terrarium last spring lived until the end of September with no attention; at the end of that period their physical condition and vigor had suffered so little that they could not be recognised after being allowed to mingle with others brought in from the field. In spite of this apparent easy acceptance of life in a terrarium, the change usually is sufficient to inhibit the egg-laying reactions, and the eggs are retained and absorbed during the next five or six weeks. Exceptionally they will be laid as under natural conditions, but only when the female has been brought from the field not more than three or four days before the time for egg-laying. It is not a question of previous impregnation or its lack, for as far as examined, all mature females have been found to have the receptacles filled with sperm some time before the egg-laying season arrives.

The character of the season has some influence on the depth beneath the surface at which the eggs are laid; in damp seasons they will be for the most part but an inch below the surface, in dry seasons they will be four or five inches below. This refers to the character of the season up to the time of egg-laying, not after.

The retention of one egg in the ovary was mentioned in the earlier paper. Later experience has confirmed the observation. The egg is always much under-sized and occurs in about one third of the females accompanying clusters of eggs in early stages of development; it is then rapidly absorbed, and must have considerable value as a

supply of nourishment for the female during her wait by the eggs. Occasionally it will almost equal the remaining eggs in size and then will be laid along with them, producing a cluster with one markedly small egg. For example, in one cluster of seven eggs, six of them had a diameter of 3.75 m.m., the remaining one of 2.75 m.m. From a difference so marked as this there is a gradual transition to the state where all the eggs of the cluster are the same size; such are about one half of all cases. The writer has twice found similarly undersized eggs of *Amblystoma;* the numbers were small, nine and eleven in the two cases, and the eggs of but two-thirds the normal size. They developed normally, producing under-sized larvae which were perfect anatomically but defective in their feeding instincts. The one lot would not feed at all; the other would snap fitfully at *Cyclops*, etc., but would not eat enough to grow or even to maintain life. This was quite striking as both lots were the species *jeffersonianum* the larvæ of which are normally voracious feeders and easy to raise. In *Plethodon* the early development of the small egg is quite normal, its fate has never been followed past the time when the larva is well formed.

One female, kept in a terrarium with her eggs, swallowed two of them, and three hours later regurgitated them. The eggs were killed by the process, whether by digestive action or by the mechanical violence it is impossible to say, for they were in the process of gastrulation at the time. This is a most critical period for the egg, its delicacy is at the maximum and very slight disturbance will cause its death. The swallowing of their spawn has been noted for many amphibia, usually where, as above, something has happened to pervert the natural instincts. Smith (1907) however, describes it as normal for *Cryptobranchus;* in this case moreover when regurgitated the eggs frequently continue to develop.

Means taken to determine the mating habits have so far been fruitless. The single observation of Wilder (1913) on *Desmognathus* is probably a close approximation to the habits of *Plethodon* in this respect.

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